AN EIGHT-WINTER STUDY OF CENTRAL IOWA BOB-WHITES [1]

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THE winter behavior and survival of central Iowa Bob-whites (*Colinus virginianus*), 1932-35, has been discussed at some length in earlier publications (Errington, 1936b; Errington and Hamerstrom, 1935; 1936). Data for five years more, 1935-40, in combination with those previously acquired, delineate a population curve that not only begins and ends with abundance peaks but also depicts seasons of scarcity. What this curve may have in common with the periodic fluctuations of grouse (Tetraonidae) and hares (Leporidae) of Canada and northern United States may be difficult to judge, but its amplitude, at least, should make it of interest from the standpoints both of conservation and biological science.

Tables 1 to 3 summarize Bob-white census figures obtained from four central Iowa areas. Techniques of investigation used were largely those of direct enumeration and "reading of sign" that have proved suitable for regular studies in this region (Errington and Hamerstrom, 1936: 310-333). Helpful information was contributed by farmers and other persons living in the vicinity of Ames; and notes taken by employees of the Des Moines Waterworks Supply Grounds (mainly by Messrs. Ben Baltzley, Lee Simmons, and Martin Haines, and made available through the courtesy of Mr. A. F. den Boer) are of supplementary value.

The Bob-white, being as a species sedentary and gregarious within limits (Stoddard, 1931; Errington and Hamerstrom, 1936), may be rather easily counted under winter conditions prevailing in north-central United States, but the validity of population figures may be affected by lack of tracking snows, by imperfectly ascertained movements of birds across the boundaries of observational areas, by interruptions of local censuses necessitated by more urgent demands of work elsewhere, and by undetected losses as from poaching. Hence, when for any reason the tabulated data are believed to be of less than standard quality, appropriate notations are added for the guidance of the reader.

Of the observational areas, the one at Des Moines (Table 1) was characterized by relatively constant environmental conditions. Non-agricultural land, it had growing on it few of the crop and weed plants of cultivation upon which the Bob-white are so largely dependent for winter food (Errington, 1936a), but this deficiency was offset by the proximity of food-bearing private fields and gardens and by feeding

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TABLE 1

Bob-white Wintering Densities, City Waterworks Supply Grounds, Des Moines, Iowa, 1932-40

Winter	Date or time of season to which census figures most closely apply	Sample area of 300 acres under regular observation		Entire Waterworks area of 1506 acres plus about 80 acres of adjacent farm land Figures from miscellaneous sources
		Only territory having known boundaries completely within sample area	Entire sample, including parts of borderline, hence imperfectly defined territories	
		Number of birds and appraisal of data if below accuracy standard	Number of birds and appraisal of data if below accuracy standard	Number of birds and appraisal of data if below accuracy standard
1932–33	Mid-Nov.	62 fair data	92 fair data	176 fair data
	Dec. 16	59	109 fair data	177 fair data
	Jan. 26	57 fair data	no data	no data
	Feb. 8	55	98	139 questionable data
	Mar. 21	55	55	no data
1933–34	Dec. 8	59	109	261 fair data
	Jan. 20	63	126	241 questionable data
	Feb. 27	49	109	215 fair data
1934–35	Nov. 23	60	82	no data
	Early Dec.	40	62	171 fair data
	Mid-Jan.	31	31	134 fair data
	Feb. 9	20	32	59 fair data
	Mar. 1	21	33	85 fair data
1935–36	Early Nov.	68 fair data	81 fair data	155 fair data
	Early Jan.	71 fair data	115 fair data	204 fair data
	Early Feb.	63 fair data	75 fair data	157 fair data
	Mid-Feb.	31 fair data	31 fair data	no data
	Late Feb.	27 fair data	27 fair data	69 fair data
1936–37	Late Nov.	40	48	
	Mid-Dec.	53	101	no data
	Late Jan.	23	23	
	Feb. 5	11	37	
	Feb. 16	9	9	
1937–38	Nov. 19	31	74	
	Dec. 21	48	84	no data
	Jan. 20	39	78	
	Feb. 23	49	66	
1938–39	Mid-Nov.	50 fair data	62 fair data	150 fair data
	Dec. 5	51	51	141 fair data
	Dec. 31	44	53	154 fair data
	Jan. 18	50	74	186 fair data
	Early Feb.	53 fair data	101 fair data	242 fair data
1939–40	Early Jan.	54 fair data	74 fair data	156 fair data
	Feb. 5	56	72	119 questionable data
	Mar. 11	26 poor data	34 poor data	no data

stations maintained by the waterworks staff. Brushy refuge cover was generally excellent in places intended for native wildlife, and the latter was given police protection from human interference. In contrast, the areas near Ames and Story City (Tables 2 and 3) were typical farm lands for which habitability for Bob-white—as concerned food and cover, at any rate—varied much from year to year and according to crop rotation as well as to differences in practices such as tree cutting, debrushing of fence rows and roadsides, plowing, and pasturing.

Population Stability

Stoddard (1931: 167-182) found that a favored area of ground in the southeastern states may be occupied by similar numbers of Bob-whites year after year, even when the composition of coveys may greatly change; and this is in keeping with the results of studies in the north-central states from 1929 to 1935 (Errington and Hamerstrom, 1936).

The latter authors listed 119 instances in which trends toward uniformity of local population levels were apparent. In 69 of these, the trends had become manifest at the beginning of the winter; in 43, through winter reduction of "surplus" birds; and, in 7, through the filling of habitat vacancies in the course of the winter. Of the central Iowa data, only those from a few well defined Bob-white range units under regular observation for many winters are strictly eligible for consideration in this connection.

It may be seen that the single territory lying within the 300-acre sample area at Des Moines (Table 1) usually accommodated between 50 and 60 birds from December to February. The decline of 1934-35 was due to experimental manipulation; that of 1935-36, to one of the most severe winter crises on record; and that of 1936-37, to egress and establishment of quarters just off the territory, which in turn was probably induced by low Bob-white densities existing on the area as a whole.

In Table 2, the principal territory west of Skunk River wintered in the neighborhood of 20 birds three of the four winters that it had initial populations up to or over that number; in the fourth winter, 1934-35, the decline seemed non-lethal and associated with population phenomena later to be discussed. The territory east of Skunk River shows little that looks like uniformity, perhaps in part because of pronounced annual variations in the winter-available food supply.

The one territory along Squaw Creek (Table 3) wintered close to 40 birds during three of the four winters it was well filled at the start; the 1934-35 decline was a clear case of eviction as a consequence of practically the entire food supply being plowed under in the fall. The limited data from the Story City area have a bearing upon the possible competitive status of the Ring-necked Pheasant (*Phasianus colchicus torquatus*) and will again be referred to.

TABLE 2

BOB-WHITE WINTERING DENSITIES OF THE SKUNK RIVER BOTTOMLANDS SOUTHEAST OF AMES, IOWA, 1932-40

Winter	Date or time of season to which census figures most closely apply	Territories usually occupied if Bob-whites winter in their vicinity		Entire area of about 1000 acres under observation
		Principal territory west of Skunk River	Principal territory east of Skunk River	
		Number of birds and appraisal of data if below accuracy standard	Number of birds and appraisal of data if below accuracy standard	Number of birds and appraisal of data if below accuracy standard
1932–33	Early Dec.	43	61	129
	Jan. 30	43	61	129
	Feb. 27	23	61 fair data	109 fair data
	Mar. 20	22	59	105
1933–34	Jan. 13	38 fair data	30 fair data	133 fair data
	Feb. 27	21 questionable data	0 fair data	58 questionable data
1934–35	Mid-Nov.	42	13	72
	Mid-Dec.	25	16 fair data	58
	Jan. 23	14	13	27
	Feb. 1	13 fair data	12 fair data	25 fair data
	Mar. 1	7	2	9
1935–36	Mid-Jan.	6 fair data	14	44 fair data
	Feb. 6	0 fair data	8 questionable data	43 fair data
	Feb. 11	0	9 fair data	41 questionable data
	Feb. 19	0 fair data	0 poor data	40 poor data
1936–37	All winter	10 poor data	0 poor data	10 poor data
1937–38	Dec. 10	0	0	12
	Dec. 23	9	0	9
	Middle and late winter	9 fair data	0	9 fair data
1938–39	All winter	12 poor data	30 to 40 poor data	40 to 50 poor data
1939–40	Dec. 28	28 fair data	44 questionable data	115 fair data
	Jan. 26	32	37 fair data	124 fair data
	Feb. 28	17 fair data	7	92 fair data

Population maxima on the above central Iowa wintering territories were largely delimited in "good quail years" by what has been called the "carrying capacity" of the land or "the level beyond which simple predation upon adult birds, their own territorial intolerances, and their tendencies to depart from coverts over-crowded with their own or some other species do not permit continued maintenance of population"

(Errington and Hamerstrom, 1936: 309). Numerical values for carrying capacity usually differed with the locality but typically remained about the same from one winter to the next on specific areas unless significant changes in environmental equations took place—*sometimes despite profound modifications in food and cover relationships.*

Food is linked with carrying capacity in the sense that enough high grade food must be available to attract, hold, and sustain the birds. The 1934-35 data for the Des Moines and Ames territories of Tables 1 and 3 reflect the abandonment of otherwise suitable habitat that may be expected when this minimal requirement is not met; but, on Midwest agricultural lands, the amounts of Bob-white foods are commonly in excess of needs except in the event of emergencies unrelated to carrying capacity as the latter has been defined. Carrying capacity may likewise be conditioned by quality and distribution of brushy cover, but individual coveys may vary astonishingly in their preference for, or dependence upon, different cover types. Certain coveys may find untenable brushy cover that may look adequate or superior to human eyes, whereas others may find habitable many patches of sparse brush or corn fields having no more cover than that provided by stalks and weeds. The declines shown by the Skunk River (Table 2) and Squaw Creek (Table 3) census figures for 1934-35 and 1939-40 were partially attributed to coveys moving to food-rich but generally cover-poor uplands situated away from the streams and outside of the observational areas.

Predation borne by wintering northern Bob-whites tends to be of incidental nature and of intensity governed by the degree of vulnerability of the birds, themselves, rather than by kinds and numbers of predators (Errington and Hamerstrom, 1936; Errington, 1937)[3]. Although populations above the carrying capacity of the land are preyed upon with conspicuous severity, carrying capacity functions as a threshold of security below which the numbers of wintering birds can rarely be forced very far through attacks of wild predators alone. Winter losses from predation on the Des Moines 300-acre sample (Table 1) have been consistently negligible. In the vicinity of Ames, the territory west of Skunk River (Table 2) lost birds from predation chiefly in 1932-33; the Squaw Creek territory (Table 3), in 1932-33 and 1939-40. On other parts of the 4200-acre Squaw Creek area, two covey groups in 1934-35 and two in 1939-40 lost considerably from predation, but the data on carrying capacities of their habitats are insufficient to permit further evaluation in this writing.

Weakness, as from injuries or hunger, may of course predispose birds to capture by enemies even when no state of overpopulation exists,

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[3] In southeastern states, Bob-white and predator relationships may differ materially from those described for the north-central region and reveal less flexibility (Errington and Stoddard, 1938).

TABLE 3

BOB-WHITE WINTERING DENSITIES OF FARM LANDS BORDERING SMALL STREAMS NEAR AMES AND STORY CITY, IOWA, 1932-40

Winter	Date or time of season to which census figures most closely apply	Area of about 4200 acres situated mainly within one mile of Squaw Creek, north and northwest of Ames		Square mile of land south of Story City having suitable habitat only in one corner
		Only well-defined territory under regular observation for full period	Entire Area	
		Number of birds and appraisal of data if below accuracy standard	Number of birds and appraisal of data if below accuracy standard	Number of birds and appraisal of data if below accuracy standard
1932–33	Dec. 17	48		
	Jan. 29	44	no data	no data
	Mar. 4	42		
	Mar. 19	42		
1933–34	Dec. 13	42		
	Early Jan.	43	no data	no data
	Feb. 27	38 fair data		
1934–35	Early Dec.	53	156	no data
	Early Jan.	7 fair data	no data	23
	Late Jan.	0	127	38 fair data
	Feb. 20	0	88	no data
	Mar. 8	0	57	31
1935–36	Nov. 28	19		no data
	Dec. 16	21	no data	no data
	Jan. 15	18		20 poor data
	Jan. 30	8		no data
	Feb. 20	4		no data
1936–37	Early Dec.	8	19 questionable data	0 fair data
	Jan. 7	6	no data	0 fair data
	Feb. 14	6	15 questionable data	0 fair data
1937–38	All winter	0	12 questionable data	15 poor data
1938–39	Early Dec.	18	45 fair data	12 to 15 all winter
	Mid-Jan.	26	39 questionable data	—poor data
	Mar. 2	10	39 questionable data	
1939–40	Late Dec.	47	231	18 fair data
	Jan. 20	31	180	15 fair data
	Early Feb.	36	157	15 fair data
	Late Feb.	40	170	15

and man may still be able to exploit populations that less-equipped predators had long found essentially unavailable.

The influence of species psychology on population levels of the Bob-white is a subject so beset by unknowns and variables that we find it hard to say how much the 1935-40 data may have to add to what has already been published (Stoddard, 1931: 167-182; Errington and Hamerstrom, 1936: 366-405; Errington, 1937). The manifestations and consequences of overcrowding may be spectacular, and there is no question that birds harassed by their fellows or forced into inferior habitats may be confronted by lethal disadvantages; to explain why limits of toleration should be definite for a given area for many winters in succession yet different on different areas is another matter, however, particularly when about the only uniformity to be seen in a local situation may relate to maxima of birds annually tolerated.

Intraspecific behavior was best studied at Des Moines, where an exceptionally stable habitat was kept filled with Bob-whites close to its evident capacity for the greater part of six or eight winters, or the whole 1932-40 period except 1934-35 and 1936-37. In all years, preliminary adjustments indicative of toleration limits on the main territory had occurred by late November or December (Table 1). Four to six coveys occupied this common territory—which was something of an ecological island of between 140 and 160 acres—during "saturation" winters, but continuous splitting and recombining of coveys and fluidity of movements seldom left coveys with any particular identity for more than a few days at a stretch, though in many ways the total population reacted as a group. Coveys from outside entered the filled-up territory on occasion, but either they did not remain or an equivalent number of birds soon departed.

Autumnal fighting between coveys has been noted alike for the Valley Quail (*Lophortyx californica vallicola*) in California (Emlen, 1939: 129) and for the Bob-white, and both species may violently exclude strangers from covey groups. Avoidance of fully populated coverts by excess birds may occur without manifestations of animosity and sometimes after close associations terminated by birds segregating into their original coveys and going their respective ways. Bob-whites of the north-central states may also, and seemingly without direct compulsion, avoid concentrations of Ring-necked Pheasants and other conspicuous animal life. Bob-whites of underpopulated areas, such as the one at Des Moines in 1936-37 (Table 1) and the two near Ames from 1934-35 to 1938-39 (Tables 2 and 3), were generally more mobile than residents that were unable to go so far without trespassing in occupied territories.

What appear to be changes in habitability of Bob-white environment may be due chiefly to increased experience of the birds as the winter progresses. Few coveys were found more than a mile from central Iowa streams at the beginning of the winter, except those fairly well situated about farm groves or the occasional grapevine tangles

along fence rows, and similar places; in late winter, 1934-35 and 1939-40, it was not unusual to encounter coveys—including large ones of 30 birds or more—in previously unoccupied farmyards and open fields one and one-half to two miles away from the streams. Among these coveys were some that were almost certainly wanderers, but the losses associated with winter-wandering of a few coveys in spacious central Iowa cornfields seem proportionally much less than those of birds drifting from one filled territory to another in areas having less food and more cover (Errington and Hamerstrom, 1936).

Since the Bob-white may nest in grassy prairie fence rows and roadsides miles from wintering quarters and as the preliminary splitting of paired birds from coveys may be observed as early as the middle of February, some of the movements into open habitat in late winter may conceivably be initiated by the approach of the breeding season. The evidence suggests, however, that the majority of the peripheral coveys gradually accustom themselves to living with less brushy cover than they require in late fall and early winter—a period of readjustment and more or less mortality from enemies.

In summer, the more general distribution of the birds, the poor visibility resulting from a profusion of ground cover, and the ephemeral persistence of carcasses are serious hindrances to the analysis of mortality in detail, and we have few reliable data on recovery of central Iowa Bob-white populations during the breeding season. Eleven years of data from an area of five square miles near Prairie du Sac, Wisconsin, indicate that the net increase of birds by late autumn and early winter is commonly in inverse ratio to the density of the spring population (Errington and Hamerstrom, 1936: 422; 1937: 17; Leopold and Errington, MS). In other words, environment that is well filled with adult birds is not likely to rear many young, with lower recovery rates under such circumstances being attributable as much as anything to accelerated juvenile mortality. Differences in kinds and numbers of enemies apparently have much more influence on seasonal recovery rates of Bob-white populations in southeastern than in north-central states (Stoddard, 1931; Komarek, 1937; Errington and Stoddard, 1938).

Irregular Fluctuations

Sudden losses from starvation may take place even during rather mild weather if the food of the birds is cut off by heavy snow or ice. Much of the 1934-35 early winter decline for the 4200-acre Squaw Creek area (Table 3) was thus accounted for, and a food crisis also followed experimental discontinuation of artificial feeding at Des Moines (Table 1) (Errington, 1936b: 560-562).

As a rule, but not invariably, northern Bob-whites can withstand cold as long as they are in good flesh (Errington, 1939: 23-7), and this

is illustrated by the Ames data for 1939-40. The extended "Indian summer" had permitted clean harvesting and pasturing by livestock of the corn field feeding grounds of a number of the Squaw Creek coveys; what little food remained was covered by snow from about the first of the year to midwinter, but few birds died of hunger before the middle of January; then, temperatures that dropped to 25° below zero (F.) eliminated in the space of less than 24 hours on January 17 and 18 almost all Bob-whites on the area not living near farm yards, feeding stations, or fields of soy beans. Our census figures show a decline of 51 birds between late December and January 20; the carcasses of 40 were found during, or just after, the cold snap. Of these carcasses, 14 collected before scavengers had eaten on them averaged 121.3 grams or from 60 per cent to 65 per cent of their "normal" winter weights, hence were in somewhat better flesh than the usual starvation victims dying at higher temperatures (Errington, 1939: 23-7). The decline of seven birds between December 28 and January 26 on the territory east of Skunk River (Table 2) mainly represents starvation losses suffered by a covey before it moved into a farm yard. Subsequent to the January, 1940, crisis, the Ames coveys wintered with slight detected mortality.

The exceedingly severe winter of 1935-36 was one of drastic losses in Iowa and southern Wisconsin (Green and Beed, 1936; Leopold, 1937; Leopold and Errington, MS), a great deal of which was due to hunger; but at least some of the lethal effect of this winter may be charged to exposure. Scott (1937) describes a covey of otherwise normal central Iowa birds reduced to helplessness by partial encasement of their heads in ice and snow. Of 14 southern Wisconsin Bob-whites found dead by Wade (1938) after the covey had been scattered just before, or during, a blizzard, five "weighed over 200 grams thawed, none less than 160 grams thawed" (Leopold, 1937: 411). The birds resident in 1935-36 on the Skunk River area (Table 2) were unusually well situated when observations were begun in the middle of January; whether these represent remnants of an earlier population is not known, but the population of the Squaw Creek territory (Table 3) really did not start dying before this time, and that of the Des Moines territory (Table 1) maintained its approximate numbers until the blizzard of February 8.

In 1939-40, a covey living about a half mile off the Squaw Creek observational area suffered another type of mortality. While on a field trip January 27, a graduate student, Mr. Leo Brown, dug five Bob-white carcasses out of a very hard snowdrift beside the snow fence of a railroad. Going out two days later, I found four more carcasses and "sign" corresponding to about four living birds. Seven intact carcasses were in good flesh, averaging 184.3 grams with no food in their stomachs. The birds had died in two loose groups (not in "huddle" forma-

tion) some days before and apparently from asphyxiation following individual imprisonment by drifting snow.

Winter losses from miscellaneous causes may vary. Shooting or trapping, which may have a pronounced effect on Bob-white population levels in some communities, is not thought to have been of consequence on the central Iowa areas during the years of the investigations. Young hatched in September or October may be at a hopeless disadvantage if cold, stormy weather comes early; some full-sized birds appear hypersensitive to low temperatures and are eliminated by the first sub-zero cold. Injuries and diseases claim individuals from time to time. Security from predation is rarely absolute, and even well situated populations may lose a few birds to enemies in the course of the winter —especially in the early part.

During the warmer months much happens concerning which we can expect to gain only fragments of information. We know broadly that the reproductive success of local Bob-white populations may be affected by climatic vicissitudes or by agricultural practices such as burning, mowing, and pasturing, and that losses of mating and incubating adults, of nests and young, may be heavy or light, but, for all of that, intercompensatory trends in breeding and loss rates may counteract many of the influences that would seem conducive to irregularities in population maintenance (see Errington and Hamerstrom, 1937, for related data and discussion).

The Question of Periodicity

Through intensive field work, we have been able to trace the preponderance of the central Iowa winter losses that we had any reason to believe due to actual death of the birds, and these losses fell with some consistency into well known and characteristically irregular types. It would therefore seem that, if any truly "cyclic" decline of central Iowa Bob-whites took place between 1932 and 1940, the causative factors must have been dominantly operative at another time of year. Kendeigh's (1933) compilation of the *Bird Lore* Christmas bird censuses for Ohio, 1908-31, show the effects of certain killing winters, but not all of the declines may be so correlated.

Failure of breeding stock to repopulate specific areas at expected rates may, for one thing, be associated with drought. In 1934, there seemed to be a rough agreement between autumn Bob-white scarcity over much of southern Iowa and the length and intensity of the spring and summer dry period in different localities (Errington, 1935); a less pronounced decrease was indicated by data from the central Iowa areas; at Prairie du Sac, Wisconsin, the recovery was "normal" for the breeding population. In view of the fact that the "cyclic" decline of grouse and rabbits in Minnesota and Wisconsin was contemporaneously in progress, the possibility of the Bob-white likewise showing general and "cyclic", rather than local and irregular, fluctua-

tions was considered but without any conviction that the Iowa declines could not be attributed mainly to the unfavorable season.

That a rainy summer may adversely affect Bob-whites is known (Stoddard, 1931: 200-202), and the unusually wet summer of 1935 was at least accompanied by rates of recovery from central Iowa breeding stock that were below expectations. Nevertheless, it is unproved that, in this case, the relationships of recovery rates to the weather were more than incidental. Recovery was "normal" for the spring density of birds at Prairie du Sac.

Winter-killing in 1935-36 had reduced breeding populations throughout the region (Green and Beed, 1936; Leopold, 1937), but neither this nor the 1936 drought, nor the two in combination, may be advanced as full explanation for the near-disappearance of Bob-whites in the vicinity of Ames. The Prairie du Sac recovery was only about half "normal" for the season's adult population—which, considering the regularity that percentages of increase on the area rose and fell inversely with the breeding densities during other years, droughts and winter emergencies notwithstanding, may suggest a depressive mechanism somewhat different from any we have hitherto succeeded in analyzing. The very poor 1936 recoveries of many species of upland small game living in the north-central region, including "cyclic" grouse and rabbits, may or may not have a significant correlation; but the data available do not refute the concept that irregular fluctuations of the Bob-white may perhaps be superimposed upon a basically, if not conspicuously, "cyclic" pattern. The similarity in the low points of the Ohio Bob-white curve (Kendeigh, 1933) and those of the hardy but violently "cyclic" Ruffed Grouse (*Bonasa umbellus*) of Wisconsin (Leopold, 1931: 142), for example, may not be due to chance.

From 1937 to 1939, Bob-white population recoveries in central Iowa and southern Wisconsin showed increasingly predictable trends, irrespective of further droughts and winter mortality, and little appeared to happen that could not be accounted for in terms of past experience.

The Competitive Status of the Ring-necked Pheasant

The Ring-necked Pheasant is not the least formidable of the exotic game birds the introduction of which has been a source of apprehension to many conservationists, and its combative prowess may even be manifested by vicious encounters with poultry cocks in farm yards or by beating off attacking enemies such as dogs or hawks. It is not strange that the occasionally authentic reports of Pheasants destroying eggs or young of ground-nesting birds should lead to conjecture as to whether some of our native wild species may thereby be driven out.

So far as the Bob-white is concerned, the aggressive traits of the Pheasant appear to be of slight direct importance. Regardless of interspecific friction that may now and then take place, Pheasants and Bob-

whites may frequently be seen using the same feeding stations and otherwise consorting without evidence of animosity. On the other hand, some types of competition between Pheasants and Bob-whites may have an adverse influence upon population levels of the latter.

The superior foraging ability of the Pheasants give them a distinct advantage over Bob-whites in such food competition as may exist between the two species (Errington, 1939). Lethal aspects of food competition during crises, however, have been observed less often than benefits to the Bob-white resulting from Pheasants—along with Crows (*Corvus brachyrhynchos*), rabbits, and fox squirrels (*Sciurus niger rufiventer*)—exposing ice-glazed or snow-buried corn and otherwise rather inaccessible foods. Dependence of Bob-whites upon "competitors" for food was especially noted on the Squaw Creek area (Table 3) during 1934-35 (Errington, 1936b: 559) and 1935-36 (Errington, 1939:34).

Competition for wintering environment on semi-wooded farm lands of southern Iowa and southern Wisconsin may favor Bob-whites rather than Pheasants insofar as the former may be better adjusted to particular habitats. From central Iowa north and west to southern Minnesota and eastern South Dakota, the prairie farm lands not only have fewer brushy coverts suitable for Bob-whites but fewer still that are not also attractive to the far more abundant Pheasants. It has been noted that, while Bob-whites may tolerate low or moderate densities of Pheasants, they tend to avoid coverts where Pheasants concentrate, essentially as they do those overpopulated with their own species. The Pheasants themselves may be tolerant of massing within much greater limits, as in fall and winter it is sometimes possible to flush hundreds at once from certain parts of tree claims, marshes, and corn fields.

The difficulties of getting reliable census figures on birds that may range as widely and irregularly as Pheasants have restricted our opportunities for even reasonably exact studies. It is neither easy to say what constitutes a sufficient number of Pheasants to cause Bob-whites to leave their coverts, nor to what degree such abandonment may have lethal consequences.

A 200-acre experimental area of the University of Wisconsin had a mixed wintering population of 47 Bob-whites and about 30 Pheasants in 1930-31 and a population of 26 Bob-whites and about 50 Pheasants in 1931-32, or a total close to 77 and 76 gallinaceous birds for two successive and comparable winters (Errington and Hamerstrom, 1936: 335, 368-369, 429-431). The carrying capacity of the tract for Bob-whites apparently declined as the Pheasant population rose; in 1931-32, a concentration of about 40 Pheasants in a 5-acre woodlot was followed by a definite withdrawal of the Bob-whites. The Bob-whites of a game management area near Ida Grove, Iowa, 1932-33, avoided the most attractive covert after about 35 Pheasants established themselves there;

and similar observations were made on neighboring land. The Story City data presented in Table 4 show a survival of 31 Bob-whites and a wintering population of about 8 Pheasants for 1934-35; 15 Bob-whites and about 27 Pheasants for 1939-40; or mixed wintering populations of about 39 and 42 birds for the two winters that are eligible for comparison.

Pheasants were present but very scarce on the Des Moines area, three being the largest number recorded for the 300-acre sample on any visit between 1932-33 and 1939-40. On the Ames areas, after several years of not doing much more than maintaining themselves at low densities, the Pheasants practically doubled their wintering populations between 1938-39 and 1939-40 (Table 4); as usual, the Bob-whites sooner or later departed from coverts frequented by more than about a dozen Pheasants, but the heaviest Bob-white survival in years does not indicate that the 1939-40 Pheasant population was seriously competitive.

TABLE 4

Comparative Wintering Densities of Bob-whites and Ring-necked Pheasants Near Ames and Story City, Iowa, 1932-40

Area	Winter	Bob-white populations		Figures arrived at for mid-winter populations of Pheasants—see text for comments
		Early winter	Late winter	
1000 acres southeast of Ames	1932–33	129	105	8 to 12
	1933–34	133	58	
	1934–35	58	9	
	1935–36	44	40	probably close to 25
	1936–37	about 10 all winter		8 to 12
	1937–38	12	9	perhaps 20
	1938–39	40 to 50 all winter		
	1939–40	115	92	35
4200 acres north and northwest of Ames	1934–35	156	57	12 to 15
	1935–36	data incomplete		about 25 to 30, with possibly a gradual increase from 1935–36 to 1938–39
	1936–37	19	15	
	1937–38	about 12 all winter		
	1938–39	45	39	
	1939–40	231	170	64
640 acres Story City	1934–35	23	31	8
	1935–39	data incomplete or of poor quality		
	1939–40	18	15	27

How abundant the Ames Pheasants would need to become to depress winter Bob-white populations and how likely the Pheasants are to increase up to this point are questions for which we as yet have no answers. Old notes indicate that, by the fall of 1921, Pheasants were just becoming established on my family's 300-acre farm west of Bruce, South Dakota, and that they reached peak numbers of about 350 by

the fall of 1927—a rise from an estimated 5 to 10 birds, or several thousand per cent in six years. This South Dakota farm presumably furnished better environment for Pheasants than exists on the Ames Bob-white areas, but Conservation Officers and other observers have also reported pronounced recent increases of Pheasants in many central and southern Iowa counties that were formerly sparsely occupied despite continued stocking. In the event that the present ascendencies of Pheasants terminate in populations averaging a bird per 2 to 10 acres over wide areas—which appear to be densities about as high as we may expect to find in midwestern "pheasant country"—a material lowering of the capacity for accommodation of Bob-white habitats may be entirely conceivable.

But even when Pheasants have all of the advantage of numbers, adaptations, and habitats, and their dominance adversely affects Bob-white population levels, it does not necessarily follow that the Bob-white will as a species be evicted from a given locality. It is still possible to find Bob-whites nearly every year in some of the strongest Pheasant range of glaciated north-central United States; data from the vicinity of Ruthven and Emmetsburg, Iowa, Hutchinson, Minnesota, and Lake Norden, South Dakota, refer to aggregates of two or three coveys of Bob-whites living along the edges of dry marshes frequented by hundreds if not thousands of Pheasants.

In the above instances, there were two apparent major reasons why competitive interactions between a thriving and another greatly handicapped species did not lead to complete replacement of one by the other, after the manner shown by the experiments of Gause *et al* with simple microcosms (Gause, 1935; Gause and Witt, 1935). The Pheasants seldom occupied with any uniformity the whole of the environment suited to Bob-whites but tended to mass along certain sides of a marsh, for example, thus leaving at nearly any time a few more or less vacant places to which Bob-whites could withdraw in comparative privacy. Then, again, the latter birds were not strictly confined to brushy habitats but were able to live more in weed patches, marshy growths, and corn fields, much as were those of the Ames coveys that displayed unusual mobility and latitude in choice of coverts.

Discussion

The statement by Stoddard (1931: 170) that Bob-white coveys tend to keep their organization of normal size through repeated combinations is emphasized by data on the possible role of "tradition" in determining toleration limits in wintering territories.

On the whole, the coverts that are occupied the most continuously seem to show the greatest year to year constancy of carrying capacity, for example, those of the main territory at Des Moines (Table 1).

The population figures for the Skunk River territories, as they are presented in Table 2, look highly variable in many respects, but the one part of the west territory that was frequented nearly every winter usually accommodated between 8 and 10 birds; the east territory, either abandoned or not occupied for five successive winters, revealed little uniformity in population levels at times when it did have birds. Three of the seven habitable Prairie du Sac, Wisconsin, territories or groups of territories that showed such definiteness of carrying capacity, 1929-35 (see Errington and Hamerstrom, 1936: 368-369, 394-395), still seem able to accommodate about the same number of birds, and these are the only ones that have not been grossly underpopulated for more than one winter in succession since 1935-36; in the course of 11 years of study, two apparent changes in carrying capacity—from one rather definite value to another—were noted, both changes following two-winter vacancies (unpublished).

The sole evidence that appears against this concept is that furnished by the Squaw Creek territory, which after four winters of underpopulation (not including 1934-35, when the territory was well filled by early December) accommodated in 1939-40 a population that compares with what were judged to be carrying capacity figures in 1932-33 and 1933-34. Six other possible territorial blocks of the 4200-acre Squaw Creek area had quite dissimilar populations in 1934-35 and 1939-40; these two seasons, with at least three low-population winters intervening, are the only ones for which our data indicate full or nearly full coverts. The existence away from the streams and gullies of large acreages of prospective or semi-habitable environment—highly attractive from the standpoint of food—is itself a partial explanation for much of the territorial laxity observed in central Iowa, but some of the differences might simply be due to failure of local habits to be carried over.

The likeliest mechanism behind these toleration phenomena seems to be dominance by veteran individuals that have their own ideas as to what constitutes desirable or safe numbers of birds in specific habitats. As long as the habitats are fairly well filled each winter, there should be a greater chance of "traditions" being retained, either through continued presence of dominant old birds or through successors having had previous local experience. It may be postulated that "traditions" die along with populations during periods of great mortality or fail to be maintained during a series of low-density years when extensive areas are left unoccupied. Interchange of Bob-whites between neighboring coveys and reorientation of old and young in different local covey groups has been demonstrated by banding (Stoddard, 1931: 169-182; Errington, 1933) as well as indicated by field observations; and it is probable that coverts well occupied for a succession of winters generally have a number of birds the responses of which to crowding in

particular places may be conditioned by former "apprenticeship" there. Emlen (1939: 125; 1940: 94-95) carried on a very detailed banding and feather-marking study of California Valley Quail populations and found that older birds had a distinct advantage in competition with the immature and the yearlings; however, he writes (letter, July 14, 1940) that there is "very little evidence of policing activity or of peck order in . . . coveys until February when, it is true, older birds generally rank highest (except when these are recent immigrants or transplants from other coveys) . . ." It is therefore conceivable that "traditions" may not represent the reactions only of veterans and that "apprenticeship" may be of shorter duration.

The possible applications of the work by Lorenz (1935; 1937) on the critical effects of early experiences of various young birds are worth considering. In the above correspondence, Emlen raises the question whether "imprinting" ("Prägung" of Lorenz) resulting from association of Valley Quail chicks with different sizes of broods or combined broods may not have a bearing upon their later flocking habits. To explain constancy of carrying capacity or of toleration limits for the Bob-white, I would think that such "imprinting" would have to be operative fairly late in life, for constancy not only seems to be maintained despite variations in size of broods and fluctuations in juvenile mortality accompanying low or heavy densities of adults but also despite the fall reorientation of the birds and occasional great changes in year-to-year food and cover relationships.

The influence of quality and distribution of food and cover on habitability of wintering environment need not be minimized in our efforts to understand Bob-white populations. We should recognize, nevertheless, that carrying capacity of given land units may be to a considerable extent a matter of what the birds themselves make it.

Summary

An eight year (1932-40) field study of central Iowa Bob-white populations not only began and ended with abundance peaks but also covered an interval of pronounced scarcity. Practically all of the traceable mortality associated with the decline took place during the winters of 1934-35 and 1935-36 and most of this proved to be of the familiar starvation-emergency types that may be expected on a greater or less scale nearly any winter; an inexplicably low rate of recovery of Bob-whites among other wild species during the breeding season of 1936, however, may suggest the operation of unknown factors, perhaps of periodic nature. Occupancy of given tracts of environment is evidently determined by the sociality of the birds as well as by food and cover conditions; and this is illustrated by Bob-white responses to crowding either on the part of their own or some other species as the Ring-

necked Pheasant, by their occasional late-winter adaptiveness in establishing themselves in food-rich fields away from the bushy fence rows, woodlots, gullies, and water courses usually frequented, and by their apparent maintenance—despite annual changes in habitats and in covey composition—of toleration "traditions" peculiar to the most regularly used winter territories.

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